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Selective predation by benthivorous fish on stream macroinvertebrates – the role of prey traits and prey abundance

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Short title: Prey selection by benthivorous fish

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Abstract

The prey selectivity of fish depends largely on traits of prey and predator. Preferable prey traits might be different for visual predators (such as drift-feeding salmonids) and rather non-visual predators (such as benthic feeders). We evaluated the explanatory power of five prey traits and prey long-term abundance for the prey selection of small benthivorous fish by analysing the macroinvertebrate community and the diet of gudgeon (*Gobio gobio*) and stone loach (*Barbatula barbatula*) in two small submontane streams. Fuzzy Principal Component Analyses, as well as electivity indices, revealed that the fish fed selectively. Prey size and feeding type were the most descriptive variables for the fish diet, followed by mean abundance, whereas microhabitat preference, locomotion mode and current velocity preference were less important. The fish preferred prey that was both small and consistently abundant, grazers and sediment feeders. Larger prey and shredders were avoided. The selection patterns of both fish species differed from those of visual fish predators but strongly resembled each other. Supporting this, in gudgeon which feeds slightly more visually than the strictly nocturnal stone loach, selectivity concerning prey traits as well as prey mean abundance was slightly more pronounced. We analysed also selectivity for prey clusters based on the three most important variables. The observed selectivity patterns concerning these clusters were less pronounced but supported the other results. The maximum (neutral) electivity index was that of gudgeon for small, abundant grazers or sediment feeders, including chironomids.

We conclude that prey selection of benthivorous fish that forage mainly non-visually can largely be explained by a small number of prey traits which probably work in combination. The prey preferences of these predators seem to be closely connected to their active foraging mode and to depend partly on the ability to detect prey visually.

49 Introduction

50 Selectivity in predation largely depends on the traits of both predator and prey
51 (O'Brien, 1979). Since selective predation is one of the strongest mechanisms structuring
52 communities (Sih et al., 1985), knowledge about the influence of prey traits on predator
53 selectivity is a prerequisite for the understanding of community processes. In stream
54 communities, fish often are the top predators. Traits of preferred prey have been analysed for
55 several predatory fish species, but mostly for visual predators. For instance, for drift-feeding
56 salmonids, particularly the drift behaviour and the body size of the prey are important (e.g. de
57 Crespin de Billy and Usseglio-Polatera, 2002; Rader, 1997; Syrjänen et al., 2011). The
58 omnivorous cyprinid *Rutilus arcasii* showed an opportunistic feeding behaviour but also a
59 positive size selectivity (Lobón-Cerviá and Rincón, 1994). To our knowledge, similar studies
60 for benthic, less visual (e.g. olfactory) fish predators are rare, despite the finding that benthic
61 fish may have a stronger predation impact on benthic communities than drift-feeders (Dahl,
62 1998). Because small-bodied benthivorous fish often feed nocturnally and thus non-visually
63 (Culp et al., 1991; Fischer, 2004; Huhta et al., 2000), they might select prey according to
64 other traits than drift-feeders do.

65 In a field experiment in Gauernitzbach and Tännichtgrundbach, two small submontane
66 streams in Central Europe, the benthic fish species gudgeon (*Gobio gobio* L.) and stone loach
67 (*Barbatula barbatula* [L.]) affected the structure of the macroinvertebrate community
68 (Winkelmann et al., 2011; Winkelmann et al., 2014). These two species differ slightly in their
69 habitat preferences and activity rhythms, gudgeon preferring pools with low current velocities
70 but foraging not as strictly nocturnally as stone loach, which in turn uses pools as well as
71 riffles for foraging (Fischer, 2004; Worischka et al., 2012; Zweimüller, 1995). In contrast to
72 gudgeon, stone loach feeds strictly non-visually and locates prey mainly by olfaction and
73 probably also via the lateral line system (Filek, 1960; Street and Hart, 1985). The numerically

dominant prey in the diet of both fish species in the above-mentioned streams were larval chironomids, as reported also by other authors (e.g. Magalhaes, 1993; Michel and Oberdorff, 1995; Smyly, 1955). Chironomids were also the most abundant group in Gauernitzbach and the second-most abundant (next to gammarids) in Tännichtgrundbach. This suggests a rather opportunistic feeding behaviour of the fish predators. However, their actual predation impact was not only mesohabitat-specific (Worischka et al., 2014; Worischka et al., 2012) but also strongly prey species-specific (Winkelmann et al., 2011; Winkelmann et al., 2007). This provokes the question whether also active prey selection by the fish predators was important in the community-structuring process. For instance, chironomids might be preferred not just due to their availability in high numbers but due to one or more ‘preferable’ traits. In the same way as trait-based sensitivity against stressors is not independently distributed over macroinvertebrate taxa (Schuwirth et al., 2015), also vulnerability against a certain predator might be determined by correlated traits. Additionally, chironomids might not be the only preferred prey item because they share such traits with other taxa. In order to separate the effects of numerical prey availability and prey traits on predator selectivity, we evaluated the importance of long-term prey abundance patterns as an additional factor during the analysis. Long-term mean abundance – even though not a prey trait - is a variable influencing the general encounter rate of a prey to a predator and thus can enhance the formation of a searching image (Tinbergen, 1960). This is not restricted to visual predation (Atema et al., 1980). The importance of abundance for prey selectivity can be seen in the switching behaviour of predators: They often respond to changes in relative prey abundance by shifting their preference to the most abundant prey and feeding disproportionately on it (Murdoch, 1969; Real, 1990). We assume that such short-term responses simply integrate over longer time periods and, together with searching images, could lead to a general preference for constantly abundant prey which goes beyond opportunistic feeding.

We investigated the prey selection by gudgeon and stone loach in Gauernitzbach and Tännichtgrundbach over four years in a reach scale field predation experiment. We addressed the following questions: (1) Do the two fish predators feed opportunistically or selectively, and do they show similar prey preferences in spite of different spatial and temporal activity patterns? (2) Can certain prey traits and/or long-term prey abundance explain feeding selectivity of benthic fish? (3) Do the fish predators prefer any groups of prey being defined by shared traits? For this purpose, we quantitatively analysed the macroinvertebrate communities of the streams and the diet composition of the benthic fish, characterizing prey taxa using five traits as well as their long-term mean abundance.

Methods

Study site and experimental design

Fish and benthic macroinvertebrates were sampled in Gauernitzbach (2nd order, 4.6 km long) and Tännichtgrundbach (3rd order, 5.6 km long), which are tributaries of the River Elbe in southeast Germany (51°06'46.63"N, 13°32'45.04"E; 51°05'12.43"N, 13°35'55.88"E). Besides being located in close vicinity to each other, the streams have very similar physical and chemical characteristics and benthic community compositions (Schmidt et al., 2009; Winkelmann et al., 2003; Worischka et al., 2012). For a large-scale field experiment on top down food web manipulation (Winkelmann et al., 2014; Worischka et al., 2014), an experimental section of 400 m was separated in each stream, using 5 mm steel mesh. After removing all fish (mainly trout stocked for angling) by backpack electrofishing (EGFI 650, Bretschneider Spezialelektronik, Chemnitz, Germany), the experimental sections were stocked with gudgeon and stone loach obtained from streams or small rivers from the same region. Both species are small-bodied, benthivorous, and inhabit mainly streams and small rivers of the Eurasian temperate zone, including the study streams. Fish density was

monitored at least four times a year by electrofishing. Losses due to winter mortality, bird predation and occasional emigration during floods were compensated by restocking the fish sections at least twice a year. Prey selection analysis was performed during two sampling periods (2005-2006, 2009-2010) when fish were present in both streams with average densities $\pm SD$ of 0.21 ± 0.19 ind m^{-2} (gudgeon) and 0.20 ± 0.17 ind m^{-2} (stone loach). These densities exceeded those before the experiment (when trout as predators and competitors were still present) but are in the same range as natural densities observed in comparable streams (Erös et al., 2003; Santoul et al., 2005). The conditions of the predation experiment are therefore well comparable to those of other, 'strictly natural' stream communities.

Sampling and processing of the samples

Six benthic macroinvertebrate samples from each stream, from three pool and three riffle locations, were collected with a Surber sampler (0.12 m^2 , 500 μm mesh size) every four weeks, throughout the entire study period. The samples were sorted under a dissecting microscope. The invertebrates were identified to the lowest practicable taxonomic level, enumerated and measured to the nearest 0.1 mm. For prey taxa including large individuals (*Ancylus fluviatilis*, *Dugesia gonocephala*, Limnephilidae and *Tipula* sp.) not only length but also thickness (the second-largest dimension) was measured in the benthos samples. The individual dry body masses were calculated using length-mass regressions (Benke et al., 1999; Burgherr and Meyer, 1997; Hellmann et al., 2013; Meyer, 1989). Gudgeon for diet analysis were collected on 21 occasions and stone loach on 22 occasions in both streams, between April and October of the four study years, but always with a time lag of at least 4 weeks after stocking. Each sampling was carried out shortly after sunrise when the fish had full guts. Five to ten individuals of each species were caught by electrofishing and killed immediately. After measuring total length to the nearest 1 mm and weighing to the nearest 0.1

g, their digestive tracts were removed, cooled between ice packs during transport to the laboratory, and stored at -18 °C. We aimed to synchronise benthos and fish sampling, attempting to complete electrofishing the day after benthos sampling. When this was not possible (i.e. the time lag exceeded 1 day), benthic macroinvertebrate densities were interpolated to the respective fish sampling date by calculating the time-weighted average of the benthic densities observed at the nearest sampling dates before and after the respective fish sampling date. Diet analyses were based on the contents of the stomach (stone loach) or anterior gut (gudgeon). Fish diet samples were processed individually, in the same way as the benthos samples, and all individuals of a fish species and a date were pooled later for calculations. The gape width (G) of the fish was estimated from total length (TL) using linear regression equations. These were derived from previous TL and G measurements of individuals from both streams (unpublished data). The equations are $G = 0.0643 TL - 0.147$ for gudgeon ($R^2 = 0.88$, $p < 0.0001$, $n = 382$) and $G = 0.035 TL + 0.889$ for stone loach ($R^2 = 0.81$, $p < 0.0001$, $n = 153$). Gudgeon in our study had a total length of 100.0 ± 24.2 mm (mean $\pm SD$) and an estimated gape width of 6.4 ± 1.7 mm. The mean total length of stone loach was 101.1 ± 30.0 mm with gape width 5.0 ± 0.5 mm.

Data analysis

Six variables describing the macroinvertebrate prey were used in this study (Table 1): five traits which we assumed to be of importance for predator selectivity and, additionally, long-term mean abundance. We chose this limited number of variables for two reasons. First, many traits are inter-correlated in benthic macroinvertebrates (Poff et al., 2006) and we tried to choose relatively independent traits *a priori*. Second, prey traits which are of any importance for visual predators only (such as drift behaviour or crypsis), were excluded. Each of the selected variables had 3 to 5 categories. Four of the traits (feeding type, locomotion mode,

microhabitat preference and current velocity preference) were taken from a trait compilation by Tachet et al. (2002); the fifth trait (body size) was parameterized from own data. We omitted some trait categories from the compilation of Tachet et al. (2002), which were not relevant for our study streams, e.g. microhabitat 'macrophytes'. The assignment of each taxon to the categories was achieved using a fuzzy coding procedure (Chevenet et al., 1994). This procedure includes the use of weightings expressing the affinity of a taxon to each of the categories. Following Tachet et al. (2002), we used weightings between 0 and 3 for feeding type and current velocity preference and weightings between 0 and 5 for locomotion mode and microhabitat preference. These weightings were transformed into relative proportions within each trait (between 0 and 1). For chironomids, we weighted their trait categories according to the relative abundances of the three dominant subfamilies Orthoclaudiinae, Tanypodinae and Chironominae (together forming 97.5% of the chironomids, based on routine emergence trap samplings throughout the study period, C. Hellmann, unpublished data) as recommended by Sheldon and Meffe (1993). Additionally, higher proportions for the feeding type category 'predator' than proposed by Tachet et al. (2002) were employed for *Gammarus* spp., *Hydropsyche* spp. and *Isoperla grammatica*, according to results of a previous study from the same streams (Hellmann et al., 2013). The trait body size was based on body mass data from our macroinvertebrate samples. It was also a convenient proxy for energy content per individual because the energy contents per mg dry mass found in the database collected by Brey et al. (2010) were similar for all prey taxa ($20.9 \pm 2.3 \text{ J mg}^{-1}$, mean $\pm SD$, $n = 37$), except for molluscs with shells, which were rarely eaten by the fish. Five size categories were defined *a priori* (Table 1). The assignment of a taxon to the size categories was done as follows: We calculated the mean individual dry body mass (geometric mean) of each taxon for each sampling date and stream separately. The obtained values were each assigned to one of the five size categories, and their relative frequencies constituted the

weightings for each taxon in the fuzzy coding. Long-term mean abundance was also coded like a trait: We assigned density values (ind m^{-2}) for each taxon at each sampling date and stream to three abundance categories (Table 1) and used the relative frequencies of the categories for each taxon as weightings.

In total, 42 benthic macroinvertebrate taxa identified in the streams, including the dummy taxon ‘others’, were assigned to the six variables (i.e. five traits plus mean abundance), forming a ‘taxa \times traits’ array (Table S1 in supporting information). For convenience, we kept the commonly used denotation ‘traits’ instead of the more general term ‘variables’. The taxon ‘others’ received average weightings for all categories. In order to avoid a biased estimation of prey selection, we included only the actual edible prey size spectrum for the fish in the calculations. This was based on a gape width of 4.5 mm, which was estimated as the lower value of $\bar{G} - 1 \text{ SD}$ of both fish species, (i.e. 4.7 mm for gudgeon and 4.5 mm for stone loach). Thus, prey individuals thicker than 4.5 mm qualified as non-edible for most of the fish; these were therefore excluded from the calculations. For Oligochaeta (except *Eiseniella* sp.) in the benthos samples we used correction factors of 0.2 for abundance and 5 for body mass. The correction was necessary because individuals of the dominant subfamily (Naidinae) tend to fragment into roughly five fragments per individual during sampling (personal observations). This leads to abundance being easily overestimated and body mass being underestimated. In the fish diet samples, no corrections were needed because only a few whole individuals and no fragments were found. Terrestrial prey was excluded from the calculations, contributing only $0.6\% \pm 1.6\%$ (mean \pm SD, all samples) to the total numeric abundance in the fish diets.

A ‘benthos samples \times traits’ array and a ‘diet samples \times traits’ array were created for each fish species. For the arrays, the fuzzy-coded categories of each of the six variables were weighted with the relative abundances of the taxa in the respective samples, for each sampling

date and stream. The different foraging habitat preferences of gudgeon and stone loach (Worischka et al., 2012) were accounted for in the benthos samples. For gudgeon which used almost exclusively pool mesohabitats, macroinvertebrate abundances from pool samples were weighted higher than those from riffle samples (97 resp. 3 %) whereas for stone loach, both mesohabitats were weighted equally. This was done in order to reflect the actual mesohabitat-specific prey availability for each fish species and so to avoid a biased selectivity analysis. We performed a fuzzy principal component analysis (FPCA) on the ‘benthos samples × traits’ and ‘diet samples × traits’ arrays (R-package ade4 version 1.5-1; Dray and Dufour, 2007; Thioulouse et al., 1997) to assess the importance of the variables, i.e. traits, for the difference between the corresponding benthos and diet samples (hypothesis 1). FPCA is a robust modification of principal component analysis (Cundari et al., 2002) and was successfully applied to fish diet analysis before (Sanchez-Hernandez, 2014; Sanchez-Hernandez et al., 2011). In order to compare the available prey in the benthos directly to the consumed prey, we combined the two arrays to one joint dataset (one below the other, Legendre and Legendre, 2012, p 702) for each fish species. Prey selection of the fish sampled on each date was calculated using the relativized electivity index E^* (Vanderploeg and Scavia, 1979), based on both prey traits and prey taxa:

$$E_i^* = \frac{W_i - (1/n)}{W_i + (1/n)} \quad (1)$$

with

$$W_i = \frac{r_i / p_i}{\sum_i r_i / p_i} \quad (2)$$

with r_i being the proportion of a prey item i in the diet and p_i its proportion in the environment, and n being the number of different prey items. E^* can have values between -1 (complete avoidance) and, theoretically, 1 (complete preference), with $E^* = 0$ indicating neutral selection. Among the large number of available electivity indices, E^* was

recommended in the reviews by Lechowicz (1982) and, with minor reservations, by Lazzaro (1987). We chose it for our study because it has the random value 0 (which we regard to be most intuitive), is robust against variation of the number of prey types and amenable to (non-parametrical) statistical testing. For the trait-based calculation of E^* we used the relative abundance data for trait categories from the fuzzy-coded ‘benthos samples \times traits’ and ‘fish diet samples \times traits’ arrays as r_i and p_i . A general challenge in electivity calculation is the occurrence of a taxon in a diet sample but not in the corresponding benthos sample. This happens occasionally with rare taxa and results in a seemingly infinite quotient between the relative abundances in the diet and in the environment. We attempted to solve this problem while maintaining a high taxonomic resolution by replacing the respective zero values (only for taxa actually eaten by the fish in this sample) in the benthos samples by a value of ‘half of the minimum detection level’ (0.5 individuals per benthos sample or 4.265 ind m⁻²). The constrained habitat use of gudgeon was, like for the FPCA, incorporated by weighting the macroinvertebrate abundances in the benthos from pools higher. In addition to analysing size selection regarding whole prey taxa, we wanted to get an idea of selection for the same size categories *within* one prey taxon. For this purpose we used the example of *Gammarus* spp., which was abundant in the benthos with a broad size spectrum and frequently eaten by the fish, calculating E^* for each size category.

In order to see whether the fish show any preferences for prey taxa sharing certain combinations of traits or variables, we grouped the prey taxa by the most meaningful variables from the previous analyses. We intended to create a clearer and more realistic classification by omitting those variables we already found to have less influence on the prey selectivity of the fish. For this purpose, we reduced the ‘taxa \times traits’ array to those three variables clearly identified as important in both the FPCA (highest loadings on the first two axes) and the trait-based electivity indices (highest ranges). We performed a hierarchical

cluster analysis based directly on the reduced array. The number of clusters was determined manually from the dendrogram by cutting at the height H with the largest difference to the two 'neighbouring' solutions, i.e. at $H = 1.62$. For each of the obtained 8 clusters, E^* was calculated. All statistical analyses and graphics were carried out using the software R (version 3.0.2, R Development Core Team, 2013).

Results

Multivariate analysis of selective vs. opportunistic feeding

Gudgeon and stone loach showed similar and pronounced prey selectivity patterns in our study (for a detailed presentation of the diet composition see Table S2 in the supporting information). In the FPCA plots of the combined datasets for benthos and gudgeon diet (Fig. 1), the first axis with an eigenvalue of 0.052 explained a major part (78%) of the total inertia (0.067) whereas the second axis contained much less information (eigenvalue = 0.009 or 14%). In the FPCA plot of the combined datasets for benthos and stone loach diet (Fig. 2), the eigenvalues of the first two axes (0.039 and 0.014) were slightly lower than for gudgeon but still explained a major part (56% and 20%) of the total inertia (0.068). The plots showed similar characteristics for gudgeon and stone loach, especially concerning the distribution of the variables (Figs. 1d and 2d). Categories of size, feeding type and abundance were most prominent whereas the other variables seemed to have a very low explanatory power. For both fish species, the arrows of the samples largely follow two main directions, corresponding to the categories 'small', 'abundant' and 'grazer' but are directed opposite the categories 'medium sized' and 'shredder'.

The differences between the corresponding diet and benthos samples (lengths of the arrows) were mostly larger than the differences among samples, indicating selective predation by both fish species. The stone loach diet samples were more widespread than those of

gudgeon, indicating a higher variability in food composition. Additionally, the arrows appear mostly shorter than for the benthos-gudgeon comparison, indicating a slightly weaker selectivity in stone loach. The FPCA plots for both fish species have further characteristic patterns in common: The benthos samples showed a seasonal pattern along the first axis and a separation between the two streams along the second axis. In summer and fall, the difference between streams was greater than in spring. The seasonal differences seemed larger than those between the streams. In the fish diet samples, however, these differences were much smaller, indicating that both fish species showed true and similar preferences independent of stream or season. In addition, the FPCA plots indicated no systematic differences between the two sampling periods (2005-2006 and 2009-2010).

Electivity indices for single prey variables and prey groups

Gudgeon showed significant electivity indices, i.e. $E^* \neq 0$, for 18 of the 26 categories, stone loach only for 6 categories (Fig. 3, Table 2, two-sided Wilcoxon tests with Holm correction, $p < 0.05$, $n = 21$ for gudgeon and $n = 22$ for stone loach). However, only few categories were preferred, most strongly ‘very small’, ‘small’ and ‘sediment feeder’ by gudgeon, and ‘sediment feeder’ and ‘microhabitat wood/roots’ by stone loach. By far more categories were avoided by the fish, most strongly ‘very large’, ‘large’ and ‘shredder’ by gudgeon, and ‘shredder’, ‘large’ and ‘medium-sized’ by stone loach. Among all prey items within the edible size spectrum, both fish predators generally preferred small prey taxa and avoided large ones. In contrast, we observed an avoidance of the two smallest size classes within the taxon *Gammarus* spp. (Fig. 4) and neutral selectivity for the larger ones. For gudgeon, a preference of abundant prey over common and rare prey was visible although not statistically significant (Fig. 3, Table 2). Stone loach, in general, showed a smaller total range of electivity indices.

The variables with the highest ranges of electivity indices between the categories were size, feeding type and mean abundance for both fish species (Table 2), and the categories yielding the highest mean E^* values (independent of their significance) belonged mostly to these three variables (Fig. 3). Because the same three variables were also prominent in the FPCA, the division into prey groups by cluster analysis was based only on them. We found eight distinct groups of prey taxa characterised by one or more categories of the three variables (Fig. 5a): very large sediment feeders (group 1, only *Eiseniella tetraedra*), rare small taxa (2, e.g. *Isoperla* sp.), rare shredders (3, e.g. *Capnia bifrons*), highly abundant grazers and sediment feeders (4, e.g. Chironomidae), highly abundant shredders (5, e.g. *Gammarus* spp.), filter feeders (6, e.g. *Hydropsyche* spp.), predators (7, e.g. *Dugesia gonocephala*) and medium-sized grazers (8, e.g. *Rhithrogena semicolorata*). Again, we observed very similar selectivity patterns for gudgeon and stone loach, i.e. a negative average selectivity for most of these prey groups (Figs. 5b and 5c, two-sided Wilcoxon tests with Holm correction, $p < 0.05$, $n = 21$ for gudgeon, $n = 22$ for stone loach). Group 4 was selected neutrally by gudgeon (sole positive E^* value) and groups 1, 4, 6 and 8 by stone loach. The electivity indices of the fish predators for each single taxon are given in Table S2 (supporting information).

Discussion

Selective vs. opportunistic feeding

Combining two different approaches (multivariate analyses and electivity indices), we evaluated the prey selection of gudgeon and stone loach as top predators in two small streams and identified the most important of six prey-characterising variables. The results concordantly suggest that the benthivorous fish foraged rather selectively than opportunistically, selecting some trait categories over others. This selectivity was observed

during all seasons even with the fish diets showing a dependency of the predators on seasonally changing prey availability. The trait-based approach seems therefore useful to detect and describe prey selection not only for drift-feeding fish (e.g. Rader, 1997) but also of benthic feeders in streams.

Importance of prey traits and mean abundance for selectivity

Two of the five analysed prey traits (size and feeding type), and long-term abundance as additional characterising variable had a strong influence on predator selectivity in our study. First and foremost, gudgeon and stone loach exhibited a strong size selectivity, preferring very small and small prey species. This was not due to gape limitation because only the edible size spectrum was included in the analyses. Such a feeding behaviour is in contrast to that of mainly visually foraging fish, which under ideal conditions prefer large, i.e. energetically favourable, prey individuals (Allan, 1981; Rincón and Lobón-Cerviá, 1995; Turesson et al., 2002). Even some non-visually foraging fish such as nocturnal planktivores showed a positive selection for larger prey, which was mediated mainly by size-dependent encounter rate (Holzman and Genin, 2005). The apparently paradoxical size selection of gudgeon and stone loach might be explained on the one hand by their preferred foraging mode, i.e. actively searching the stream bottom (Filek, 1960; Worischka et al., 2012), which makes size-dependent activity of the prey less important for encounter rate. On the other hand, we may also take into account that small taxa are usually more abundant than large taxa (Meehan, 2006). A selection of small prey therefore may indirectly select for abundant prey, and *vice versa*. This was observed with gudgeon and stone loach, which showed a relative preference not only for the categories ‘very small’, ‘small’ and ‘abundant’, but also for small-bodied and abundant prey taxa (chironomids and simuliids, respectively, see Table S1 and S2 in the supporting information). Small size classes of one abundant prey taxon, *Gammarus*

spp., were rather avoided by both fish species, but they were also less frequent in the benthos than the medium and large size classes during the sampling periods. Therefore, we suspect that the apparent size selectivity was in fact selectivity for abundant prey taxa. We assume that this behaviour could be a number-maximizing feeding tactic, comparable to that found by Rakocinski (1991) for small darter species. In Optimal Foraging Theory (Emlen, 1966; MacArthur and Pianka, 1966), prey size determines energy content and handling time and prey abundance determines the encounter rate. An increasing selectivity for larger (i.e. energetically more profitable) prey with increasing absolute prey abundance (Werner and Hall, 1974) is likely only as long as handling time is constant and prey is encountered simultaneously, a typical situation for planktivorous fish. For small benthivorous fish species, it is more realistic to assume that handling time is relatively long and increases with prey size, prey is encountered sequentially, and satiation occurs sooner during feeding. Under these conditions, an increasing preference for smaller prey would be the most efficient feeding tactic (Gill, 2003; Hart and Ison, 1991).

Thus, the consideration of size and abundance in combination seems to be necessary in prey selectivity analyses. Switching as a short-time response to fluctuations in relative prey abundances seems to be common in fish predators (Hughes and Croy, 1993; Ringler, 1979; Zhao et al., 2006) and probably also occurred in our study system. However, the fuzzy-coded long-term mean abundance categories we used in our analysis represent more information than just the momentary relative abundance, namely whether a prey is regularly encountered by the predator with a high probability. Therefore, we assume that the general preference of gudgeon and, to a lesser extent, also of stone loach for highly abundant prey can be explained only with a combination of at least two mechanisms, a fast-acting one (switching) and a slow one. The latter could be a certain 'inertia' of the searching image (Tinbergen, 1960), as learning processes, for instance the acceptance of novel, rare prey types among known, highly

abundant prey types, are often associated with a time delay (Fraser et al., 2013). Another learning process is the recognition of non-profitable patches in heterogeneous environments. Here, predators seem to need much more time to identify such patches regarding prey abundance than regarding prey body mass (Esposito et al., 2010). The search mode of gudgeon and stone loach as benthic feeders is probably strongly patch-related. It is therefore conceivable that the short-term preferences of gudgeon and stone loach have merged over time into a general preference for abundant prey. Supporting this line of thought, Johnson et al. (2007) as well as Uieda and Pinto (2011) indicate the highest electivity indices of fish predators for the (overall) numerically dominant prey in the respective benthic community. In more homogeneous pelagic predator-prey systems, where visual foraging is also more important, prey ingestion more often seems to be proportional to relative prey abundances, or the preferred prey is not the most abundant one (e.g. Storch et al., 2007; Verliin et al., 2011).

Macroinvertebrate feeding type was, next to size, the most important trait influencing the prey selectivity of the fish; grazers and sediment feeders were generally preferred in our study. In accordance with our findings, benthic grazers in stream enclosures were subject to a strong top-down influence by benthivorous sculpins, which was partly explained by their body size and partly by their feeding habit and resulting exposition (Rosenfeld, 2000). The feeding modes grazing and sediment feeding are often closely associated in benthic macroinvertebrates, i.e. many taxa use both (see Table S1 in the supporting information). In contrast, the category 'shredder' was, although very common among the benthic macroinvertebrates in the studied streams and also in the fish diet, negatively selected by the fish. This was true even for highly abundant shredders as can be seen from the cluster-based selectivity analysis, underlining the high relevance of prey feeding type for predator selectivity. In a previous field experiment in Gauernitzbach (Winkelmann et al., 2007), gudgeon had a much stronger predation effect on *Gammarus pulex* (an important shredder)

than on *Rhithrogena semicolorata* (an important grazer). A special characteristic of macroinvertebrate shredders is that they are able to use their food source as refuge. The effectiveness of this predator avoidance strategy has been shown by Szokoli et al. (in press).

The prey traits locomotion mode, microhabitat preference and current velocity preference were of lower importance for prey selection in our study although all three may theoretically influence the encounter rate from the prey side. For actively searching benthic predators like gudgeon and stone loach, the locomotion mode of the prey might be less important than for ambush predators or slow-moving active predators (Muotka et al., 2006; Sih and Moore, 1990). Microhabitat preferences of benthic macroinvertebrates in streams may influence predator encounter rate especially if they include the use of refuges such as crevices (Fairchild and Holomuzki, 2005). This seems to have played a minor role in the studied streams. The positive electivity indices for 'microhabitat wood' may result from a temporary preference for simuliids and other abundant taxa with a high affinity to this microhabitat type. Even though current velocity preferences of the fish were already accounted for in the calculations, the electivity pattern of gudgeon concerning current velocity preference as a prey trait was still stronger than that of stone loach, indicating that typical riffle taxa were avoided by gudgeon also when they occurred in pools.

Selectivity for prey groups

Chironomids, numerically dominating the diet of both fish predators in the studied streams, are small and highly abundant and, mostly, also grazers or sediment feeders. They might share this 'preferable' combination of characteristics, which is equivalent to a trait syndrome *sensu* Poff et al. (2006) with other prey taxa. Instead of prey selection based on single prey variables or taxa, our third hypothesis therefore focussed on selection for prey groups sharing combinations of variables. We found less distinct selectivity patterns than

Yamada et al. (2010), who could largely explain age-dependent diet composition of marine seagrass-bed fishes with a model approach combining taxonomic and trait-based prey groups. However, the patterns that we observed are in concordance with the other results of our study, especially concerning selectivity for small and abundant taxa and the contrary influence of the feeding types ‘grazer’/‘sediment feeder’ and ‘shredder’.

Consequences for predator coexistence

The prey selectivity differences found between the fish species correspond to differences in their habitat use and foraging mode. For gudgeon, which partly detects prey visually and has a greater affinity to pools (Worischka et al., 2012), we observed generally a more distinct selectivity (positive and negative) than for stone loach. This concerned single prey traits, for instance prey size or current velocity preference, but also prey groups sharing trait combinations. A possible explanation for the lower degree of selectivity in stone loach might be its strictly non-visual and benthic foraging mode (Filek, 1960; Worischka et al., 2012). Compared to drift-feeding fish, much less is known about the preferred prey traits for benthic feeders. The selectivity patterns we found for two benthic predators differed clearly from those of drift-feeders and other visual predators (e.g. Rader, 1997) but resembled each other remarkably, despite the above-mentioned differences. Gudgeon and stone loach even seemed to select a similar spectrum of prey variables in both studied streams whereas the benthic samples from the streams differed regarding these variables. The co-occurrence of two top predators with such similar prey preferences suggests a strong food competition. However, competition seems to be weakened by the different spatial and temporal activity patterns (gudgeon being temporally flexible and stone loach spatially) which might have facilitated resource partitioning (Worischka et al., 2012). Such competition-minimizing mechanisms have been observed also in other studies (Copp, 1992; Greenberg, 1991;

Sanchez-Hernandez et al., 2011). But even without a strong resource partitioning, the shared use of a highly abundant main food resource, i.e. chironomids, probably allows the two predator species to coexist. Therefore, the observed prey selectivity patterns are most probably advantageous for both fish predators.

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670 **Tables**671 **Table 1** Variables and their categories characterising prey, as used in calculations and plots.

Trait abbr.	Trait (explanation)	Categories abbr.	Categories (explanation)
abu	mean abundance (<i>log10</i> of mean abundance (ind m ⁻²))	a1	low (≤ 1)
		a2	medium ($1 \dots \leq 2$)
		a3	high ($2 \dots \leq 4$)
fty	feeding type	ff	filter feeder
		fg	grazer
		fp	predator
		fse	sediment feeder
		fsh	shredder
loc	locomotion mode	lc	crawling
		ld	digging
		lse	sessile
		lsw	swimming
mha	microhabitat	ma	algae/macrophytes
		mg	gravel/sand/silt
		ml	leaf litter
		mm	mud
		ms	stones
		mw	wood, roots
size	size (<i>log10</i> of body mass (mg dry))	s1	very small (≤ -2)
		s2	small ($-2 \dots \leq -1$)
		s3	medium ($-1 \dots \leq 0$)
		s4	large ($0 \dots \leq 1$)
		s5	very large ($1 \dots \leq 2$)
vel	current velocity preference	v1	zero (0 ms^{-1})
		v2	low ($< 0.25 \text{ ms}^{-1}$)
		v3	high ($> 0.25 \text{ ms}^{-1}$)

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Table 2 Range of the electivity indices E^* of gudgeon and stone loach for the single categories within each variable (mean of all sampling dates and streams $\pm SD$) and results of Wilcoxon test with Holm correction, p_{adj} values < 0.05 (broad) indicate that E^* was significantly different from 0 (see also Fig. 3).

Variable	Gudgeon			Stone loach		
Category	Range of E^*	V	p_{adj}	Range of E^*	V	p_{adj}
abu	0.57 \pm 0.32			0.39 \pm 0.25		
a1		36	0.043		114	1.000
a2		8	0.001		8	0.001
a3		189	0.072		159	1.000
fty	0.61 \pm 0.24			0.67 \pm 0.25		
ff		167	0.456		130	1.000
fg		167	0.456		175	0.596
fp		58	0.322		17	0.005
fse		207	0.011		32	0.046
fsh		7	0.000		19	0.007
loc	0.35 \pm 0.18			0.38 \pm 0.23		
lc		4	0.000		48	0.316
lc		27	0.015		80	1.000
lse		228	0.000		162	1.000
lsw		38	0.050		59	0.703
mha	0.37 \pm 0.16			0.34 \pm 0.14		
ma		68	0.456		63	0.912
ml		15	0.003		82	1.000
mm		80	0.687		105	1.000
msa		101	0.711		37	0.093
mst		210	0.007		156	1.000
mw		209	0.008		206	0.019
size	1.03 \pm 0.44			0.85 \pm 0.34		
s1		201	0.020		165	1.000
s2		207	0.011		176	0.596
s3		17	0.004		17	0.005
s4		11	0.001		31	0.045
s5		12	0.006		55	0.596
vel	0.24 \pm 0.14			0.25 \pm 0.19		
v1		203	0.016		109	1.000
v2		88	0.711		156	1.000
v3		10	0.001		80	1.000

Figures and legends

Figure 1 FPCA of the samples of benthos and gudgeon diet. (a) – (c) Plots of the samples, arrows connect the benthos sample (arrow origin) with the respective diet sample (arrow head) for each date and stream. All three plots represent the same dataset, only grouped by (a) stream with G = Gauernitzbach and T = Tännichtgrundbach, (b) season with 1 = spring, 2 = summer, 3 = fall, and (c) year with 05 = 2005 etc. (d) Plot of the variables and the eigenvalues of the axes for this FPCA. Bottom right: scaling of the axes for all four plots. Trait abbreviations see Table 1.

Figure 2 FPCA of the samples of benthos and stone loach diet. (a) – (c) Plots of the samples, arrows connect the benthos sample (arrow origin) with the respective diet sample (arrow head) for each date and stream. All three plots represent the same dataset, only grouped by (a) stream with G = Gauernitzbach and T = Tännichtgrundbach, (b) season with 1 = spring, 2 = summer, 3 = fall, and (c) year with 05 = 2005 etc. (d) Plot of the variables and the eigenvalues of the axes for this FPCA. Bottom right: scaling of the axes for all four plots. Trait abbreviations see Table 1.

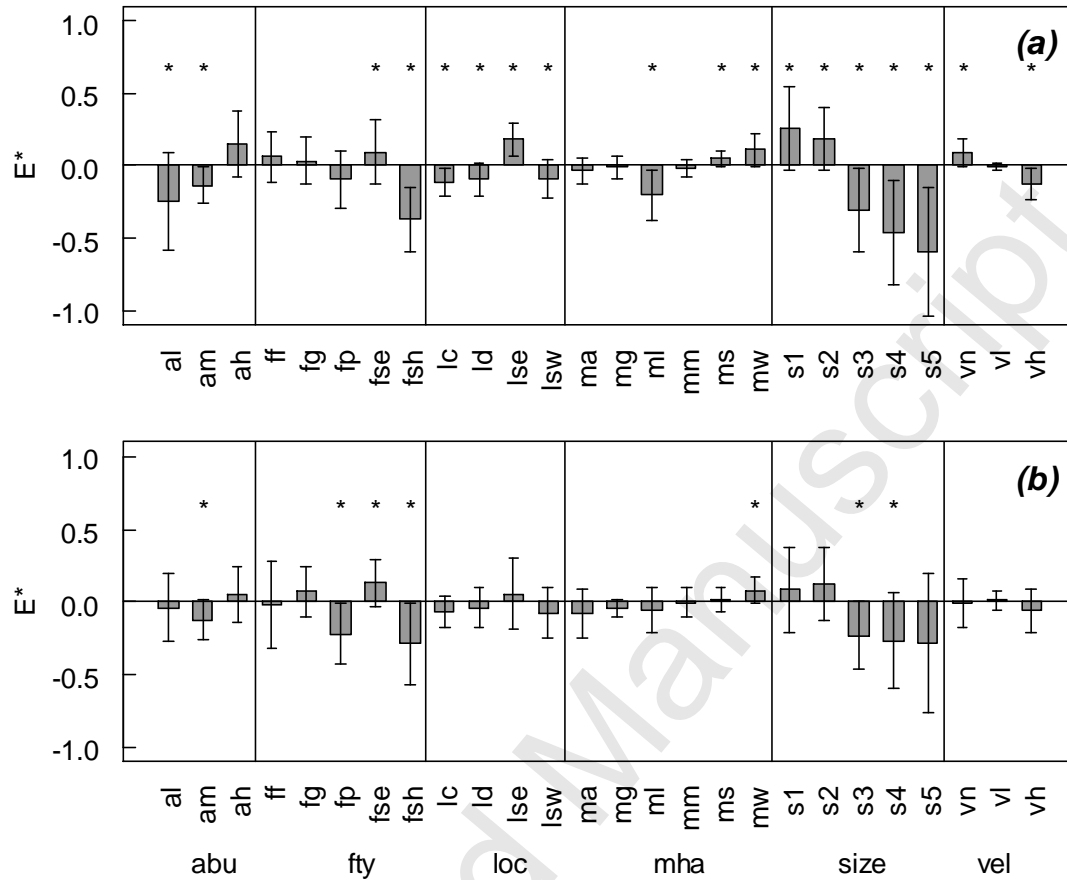


Figure 3 Electivity indices E^* of gudgeon (a) and stone loach (b) for the categories of the variables mean abundance (abu), feeding type (fty), microhabitat preference (mha), locomotion type (loc), size, and current velocity preference (vel). Black lines = median, black squares = mean, boxes = quartiles, whiskers = range. Trait and trait category abbreviations see Table 1. Asterisks indicate E^* values significantly different from 0 (p -values see Table 2).

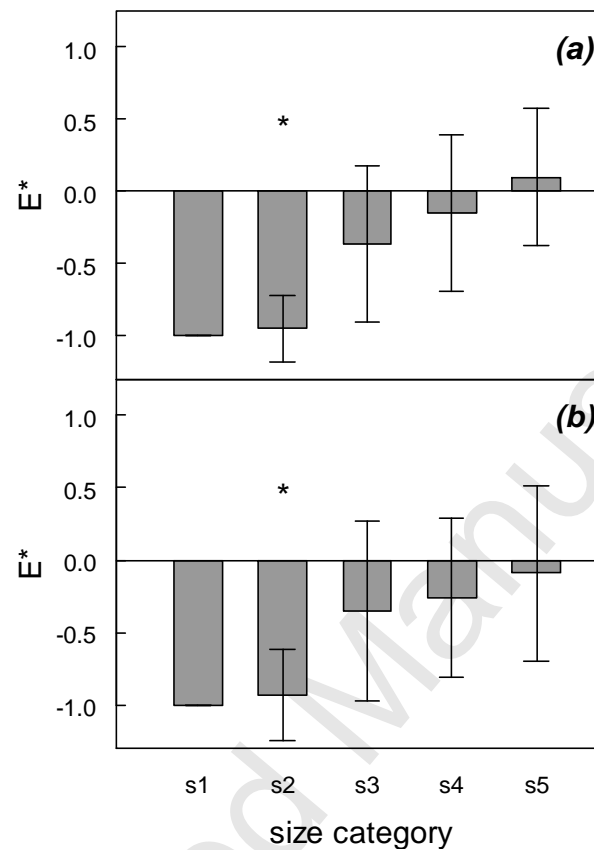


Figure 4 Electivity indices E^* of (a) gudgeon and (b) stone loach for size classes of *Gammarus* spp. in the streams Gauernitzbach and Tännichtgrundbach (mean \pm SD of all sampling occasions). Size classes correspond to size categories in Table 1. Asterisks mark significant differences from 0 (s1 not tested).

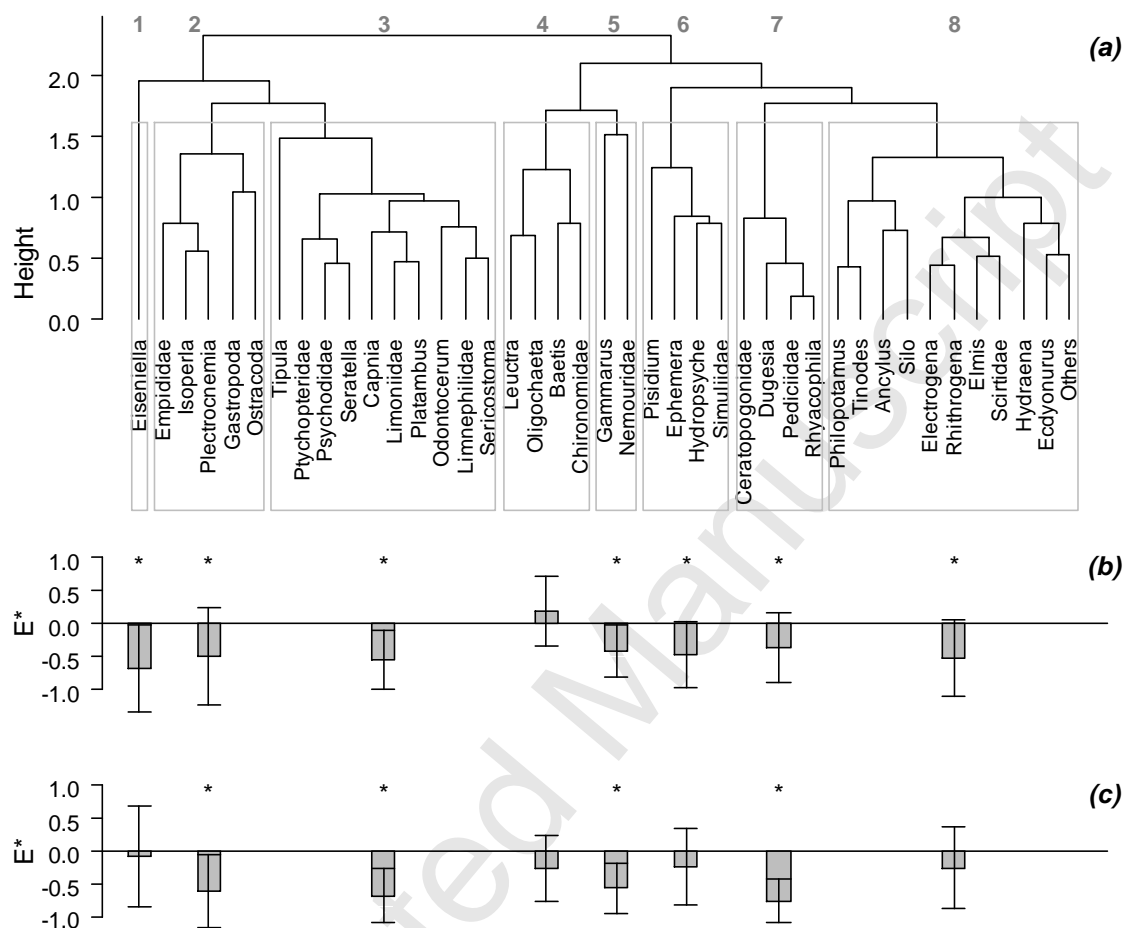


Figure 5 Hierarchical cluster analysis (a) of the ‘taxa × traits’ array (grey numbers and rectangles mark the prey groups) and electivity indices E^* of gudgeon (b) and stone loach (c) for each prey group (mean \pm SD of all sampling occasions, gudgeon $n = 21$, stone loach $n = 22$). E^* values significantly different from 0 are marked with asterisks.

